Tree loss impacts on ecological connectivity: developing models for assessment.

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Abstract

Trees along linear features are important landscape features, and their loss threatens ecological connectivity. Until recently, trees outside of woodlands (TOWs) were largely unmapped however; the development of innovation mapping techniques provides opportunities to understand the distribution of such trees and to apply spatially explicit models to address the importance of trees for connectivity. In this study, we demonstrate the utility of models when investigating tree loss and impacts on connectivity. Specifically, we investigated the consequences of tree loss due to the removal of roadside trees, a common management response for diseased or damaged trees, on wider landscape functional connectivity. We simulated the loss of roadside trees within six focal areas of the south east of the UK. We used a spatially explicit individual-based modelling platform, RangeShifter, to model the movement of 81 hypothetical actively dispersing woodland breeding species across these agriculturally fragmented landscapes. We investigated the extent to which removal of trees, from roadsides within the wider landscape, affected the total number of successful dispersers in any given year and the number of breeding woodlands that became isolated through time. On average roadside trees accounted for less than 2% of land cover, but removing 60% of them (~1.2% of land cover) nevertheless decreased the number of successful dispersers by up to 17%. The impact was greatest when roadside trees represented a greater proportion of canopy cover. The study therefore demonstrates that models such as RangeShifter can provide valuable tools for assessing the consequences of losing trees outside of woodlands.

Keywords Connectivity; tree disease; modelling; RangeShifter; scattered trees; corridors

Taxonomy Habitat Management, Landscape Ecology, Ecological Modeling, Conservation Ecology

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Order of Authors Roslyn Henry, Stephen Palmer, Kevin Watts, Ruth Mitchell, Nick Atkinson, Justin Travis

Suggested reviewers Cécile Albert, Nick Leimu-Brown, Laura Jane Graham, Anne Mimet, Bjorn Reineking

Submission Files Included in this PDF

File Name [File Type]

henry_et_al_coverletter_revision.docx [Cover Letter]

henry_et_al_responsetoreviewers.docx [Response to Reviewers]

henry_et_al_highlights.docx [Highlights]

henry_et_al_revised.docx [Manuscript File]

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Research Data Related to this Submission

There are no linked research data sets for this submission. The following reason is given:
Data will be made available on request

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Dear Professor Recknagel,

We are re-submitting our manuscript titled, "Tree loss impacts on ecological connectivity: developing models for assessment", following major revisions.

Following reviewer suggestions, we have reframed the manuscript to focus on the importance of trees as elements for connectivity under more general threats, and thus removed the focus on ash dieback. Trees along infrastructure features such as roads, railways and watercourses occupy an increasing proportion of all trees outside of woodlands, but the impact of roadside tree loss on wider landscape connectivity, due to felling in response to tree disease or climate induced mortality, remains unexplored. Furthermore until recently, trees outside of woodlands have been largely unmapped however, with the development of innovation mapping techniques there are now opportunities to explore the importance of such trees. Thus the novelty of our study remains unchanged; we use a spatially explicit individual-based model which utilises innovative high resolution mapping data, to consider the impact of the loss of non-woodland trees on wider ecological landscape connectivity, as a first step towards understanding the most appropriate management and recovery response.

We do not combine another model to locate sick trees and ash dieback spread to create patterns of tree loss as suggested by reviewer 1, nor do we map the virtual species modelled on to species that utilise ash trees as suggested by reviewer 2. Both approaches would now lie beyond the context of the revised manuscript, but they remain potentially interesting avenues for future work, and we highlight this in the discussion.

We believe the revisions have enlarged the scope of the paper to highlight the importance of trees for connectivity under multiple threats, and thus the paper is even more relevant to the readership of Ecological Informatics. We look forward to your evaluation of the revisions.

Yours sincerely

Dr Roslyn Henry (on behalf of all the authors)

Comments from the editors and reviewers:
-Reviewer 1

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The authors present an application of a spatially explicit modelling platform (RangeShifter) to investigate the ecological implications of tree removal following disease (ash dieback). With tree disease such as ash dieback an increasing concern, this is a timely research paper. I do however recommend some rewriting of the manuscript to enable ease of understanding.

General comments

1. **The manuscript in its current form is quite difficult to read. There seems to be some information missing, and then some information that feels superfluous. I have made specific recommendations below.**

We have addressed the recommendations of all three reviewers and hope that along with the reframing of the manuscript it is easier to follow.

2. **I am unsure of the novelty of the application. This seems more of a reframing of the use of RangeShifter in landscapes of differing compositions, but with roadside trees randomly removed to change the focus to tree disease. I feel the paper would be more effective if it were coupled with models of disease spread to create realistic patterns for analysis. This is suggested as a future avenue of research in the discussion, but I do think this is where the novelty would be. The authors find that differences between replicates account for up to 30% of the variation – suggesting that spatial structure is important for the conclusions. Therefore I would suggest that analysing realistic patterns of tree loss (as opposed to random) would make more sense.**

We have followed reviewer 3's recommendation and changed the manuscript to focus on tree loss and connectivity rather than ash dieback per se. Thus we have reframed the paper as assessing the importance of trees as elements for connectivity, under different threats and the use of Rangeshifter as a tool to do so. We do not combine another model to locate sick trees and ash dieback spread to create patterns of tree loss as this would now be beyond the context of the revised manuscript. Furthermore given the multiple threats to trees, disease, climate and management, it would be difficult to determine how 'realistic' patterns will look, and we therefore keep the random approach for this initial study of tree loss and connectivity. We do however continue to highlight in the discussion the potential coupling of models of disease spread to identify patterns of tree loss to models analysing connectivity as an avenue for future work. Furthermore, trees along infrastructure features such as roads, railways and watercourses occupy an increasing proportion of all trees outside of woodlands, but the impact of tree loss on wider landscape connectivity, due to felling in response to tree disease or climate induced dieback, remains unexplored. Until recently, trees outside of woodlands were largely unmapped however, with the development of innovation mapping techniques there are now opportunities to explore the importance of such trees. Thus the novelty of our study is that we use a spatially explicit individual-based model (typically connectivity studies hitherto use approaches based on graph theory) which utilises innovative high resolution mapping data to consider the impact of the loss of these trees on wider ecological landscape connectivity, as a first step towards understanding the most appropriate management and recovery response.

2. **It would be helpful to explicitly state the question(s) you are answering and your predictions/hypotheses in the last paragraph of the discussion.**

We have altered the final paragraph of the introduction to outline our research question more specifically.

3. **Are 10 replicates enough for the landscape and demographic replicates? It would be useful to get an idea of the distribution of values (for successful dispersers and patch isolation).**

   For all tree removal scenarios (20%, 40%, 60%) on all squares, demographic replicate, together with its interactions with the four varied factors, accounted for < 0.01% of the variance in the number of successful dispersers and isolated patches (Appendix A, Tables A3,A4,A5). Therefore, we believe that 10 demographic replicates are in fact more than sufficient. Landscape replicates indeed accounted for up to 30% of the variation, indicating that the spatial pattern of tree removal is important for connectivity, and we believe this an interesting point in itself. However, increasing the number of landscape replicates would be unlikely to alter our main results; indeed testing a great number of replicates in the initial stages of the study did not greatly affect the results. Running an increasing number of replicates always comes at the expense of computing time (running the 81 species and all the replicates over 6 different landscapes already resulted in over 150000 simulations). We feel that our choice of 10 demographic replicates and 10 landscape replicates is sufficient to generate robust results while maintaining tractable computing timescales. Furthermore with 81 species, 6 tiles, baseline scenarios and three removal scenarios the distributions of replicates could be shown for a possible 1458 different combinations. Therefore rather than present the distribution of values for replicates, for ease of reading, we chose to present the mean, min and max proportion of successful dispersers/isolated patches relative to the baseline landscape for each tree removal scenario on each square.

4. **General comment on the discussion: the results are represented and interpreted, but with almost no connection to related literature. I suggest interpreting the results in the context of other studies.**

This is a good point and we have now improved the first three paragraphs of the discussion to incorporate existing related literature when we interpret our results.

Specific comments

L14-15: What questions do you plan to address?

L24-25: What species groups are the theoretical species meant to represent?

We have altered the abstract to address the above two points.

L33: Be more specific about the type of model RangeShifter is.

We now write '…spatially explicit individual-based modelling platform, RangeShifter' in the abstract line 18.

L82: change to "circuit theory (e.g. Circuitscape, McRae et al. 2008)" – when Circuitscape is mentioned on line 88 it comes from nowhere.

Done.

L83: Add to the end of the SMS sentence "which is embedded in RangeShifter" – it makes the introduction match up more clearly with the abstract and methods.

Done.

L78-98: It makes more sense to have this paragraph after the paragraph L99-120.

We have restructured the introduction following comments from all reviewers.

L122-126: This paragraph is out of place, and repeated later.

This paragraph has been removed.

L175: Change "those that fell out with" to "those that did not fall within the boundaries of"

Done.

L179: What are the associated costs? Perhaps include these in the text and/or Figure 2 legend.

The costs can be found in Table 2, we have adjusted the text to direct the reader to table 2.

L228-231: The bit in the brackets confused matters with the reading of the methods. I suggest moving to after "30 removal scenario landscapes" and changing to (10 replicate landscapes for each of the 20%, 40% and 60% roadside tree removal scenarios).

We have changed this.

L233: Why the 10 year burn-in? If standard provide a reference, if not provide justification.

The burn-in period is to allow the population dynamics within the model to stabilise. Burn-in periods vary depending on the model and simulations, and initial testing indicated that 10 years for sufficient for the simulation runs for the study. We have added a sentence to the methods to justify this.

L244: Which function/package did you use? Also, make sure to cite R and any packages used – it helps with reproducibility and also provides credit to package developers.

The package information and citations have been added.

L281: I make this 5% and not 9%

Thank you, this has been changed.

L283: I make this 0.7% instead of 3%. Also where are the results for HM and PR?

Thank you, this has been changed. For ease of reading we have included the main effects columns only. Interactions between factors were (with the exception of carrying capacity and per-step mortality risk for successful dispersers noted in the text) relatively unimportant and thus we chose not to present them.

L288: Given for each scenario and square the minimum change in number of isolated patches is negative and the maximum is positive, the mean is not really meaningful – yes the mean change is limited, but that's because some spatial configurations allow for a more substantial decrease and some an increase. Perhaps it's better to discuss the min/max in the results and not present the

mean. This again provides an argument for showing the distribution of the values obtained for the replicates.

As highlighted above with 81 species, 6 tiles, baseline scenarios and three removal scenarios the distributions of replicates could be shown for a possible 1458 different combinations and thus for ease of reading we chose to present the mean, min and max. We have however changed the text to discuss the min/max now rather than the mean and highlight the reviewers point in L315. We also now discuss the positive and negative results in the context of other studies in the discussion L380.

L295: add "compared to the baseline" after "isolated patches"

Done.

L296: Interactions are not shown in the table.

Similar to the table for successful dispersers; for ease of reading we have included the main effects columns only. Interactions between factors were relatively unimportant and thus we chose not to present them.

L297: Keep consistent with the rest of manuscript and change "DP" to "directional persistence".

Done.

L309: change to "mean proportional reduction"

Done.

L361-378: Where 'models' are mentioned to investigate the impact of tree loss on foraging habitat and shelter does this mean the same modelling approach? If so please explain how it could be applied. My understanding is that RangeShifter models dispersal in terms of emigration, transfer and settlement and I'm not sure how forage/shelter fits in to the modelling platform. If not, this paragraph should be removed or adapted.

We have removed this text as it was indeed confusing.

Table 3:

1. **Explain why some of the numbers are in bold.**

   Values >0.2 are highlighted in bold. We have added this to the figure legends.

2. **Results for PR are missing from the table**

   We have added the PR column.

Table 4:

1. **PR is missing from the caption**

We have added this.

2. **Use the same layout as table 3 because it's easier to read (e.g. the horizontal lines demarcating the squares)**

Done.

3. **What does the residuals column represent?**

We have removed the residual column as it was unnecessary.

4. **Where is the interaction column?**

For ease of reading we have included the main effects columns only. Interactions between factors were relatively unimportant and thus we chose not to present them.

Figure 2: move (a) to between “showing” and “the” – makes it clearer that both images are the same grid cell.

Done.

Figure 5 and 6 – perhaps include the standard errors as error bars.

The standard error bars are too small to be seen on the graph, the standard errors are however presented in the appendix tables.

-Reviewer 2

-

General comments.

The authors create 81 virtual species by considering all possible combinations of four factors (carrying capacity, perceptual range, directional persistence, unsuitable habitat mortality) at three levels. Their conclusions are based on the mean proportion of these 81 virtual species that successfully disperse. I am concerned that we have no information on the proportion of 955 species that use ash trees or the 45 species are that are assumed obligate on ash that have each of these 81 different factor combinations. It is possible that a large proportion of species have very similar combinations of these four factors – in particular the 45 that are ash-obligates. Similarly there may be factor combinations that occur extremely rarely in the real world. I think that it is therefore misleading to conclude that removing 60% of roadside trees could decrease the number of successful dispersers by up to 17% (Line 306). I think that this study shows instead that 17% of 81 possible combinations of four factors relevant to dispersal would decline. If none of the 955 species that use ash possess any of these factor combinations then it is possible that there would be no decline of species at all. Alternatively, if these combinations of factors are common in ash-using species the decline may be much more severe than predicted. We know how many of the species that use ash are birds, vascular plants, lichens etc. It ought therefore to be possible to include a rough idea of how the virtual species types created by the authors map onto the characteristics of real species.

Following reviewer suggestions, we have reframed the manuscript and thus removed the focus on ash dieback. We therefore no longer believe it necessary to map the virtual species on to species using ash trees. We agree with reviewer 2 that the results will be relevant to only certain species however, and we acknowledge this in the last paragraph of the discussion. However, we also highlight that there are insufficient data on the dispersive characteristics of woodland species (ash dependent or otherwise) and thus until such data become available it would be difficult to do so. Rather than include only some 'realistic' assumptions mixed with theoretical assumptions, for parsimony, we create entirely virtual species. This also has the advantage of allowing investigation of parameter space. If, indeed, future empirical work on quantifying dispersive traits in woodland species discovers that such species do possess traits (that are highlighted in this study) that may make them vulnerable to tree loss then this could provide the basis for management and act as an early indicator of risk.

I was also concerned that they only attempted to model "active" species, and many of the most at-risk ash associated species are poor dispersers (eg lichens) - specifically because they tend to get stuck in little habitat pockets and end up very range-restricted.

In this paper we have deliberately focused on investigating the potential impact that the loss of roadside trees might have on the connectivity of species for which trees forms a positive component of the matrix. Our focus is thus on species that have the capacity to, at least occasionally, disperse successfully between the patches of woodland that, for these species, we consider breeding habitat to be. The reviewer is correct that there are many species that have very poor dispersal ability. For these species, the trees outside of the woodlands are likely to provide key patches of habitat that can form stepping stones via which the species can maintain connectivity between woodlands – though this is a different type of connectivity as it occurs over multiple generations.

There are quite a few unreferenced assumptions in the model that could potentially have quite a big effect on the results: eg. Why did the authors assume that species would only reproduce in "breeding patches"? There are, I am sure, a number of species that breed in roadside trees. I would like to see more justification for this and other assumptions, or at least to see them varied to see how strong an effect they have.

This relates to the point above. We have decided to restrict ourselves here to species that need a woodland patch for reproduction. For these species, the trees outside of woodland improve the permeability of the matrix. We have not focused on species for which single trees outside of woodland provide suitable breeding habitat. However, we recognise that for a set of species, individual trees will provide important habitat. In future work, we will extend our modelling to investigate this. It requires first some technical developments as this will substantially increase both the number of suitable patches of habitat on the landscape and the total population sizes, requiring greater computing power. We have edited the manuscript such that our current focus is clearer L160.

I feel that it is important that the authors include a second analysis where trees in the "breeding patches" are also reduced. They mention this as future work, but I think it would be interesting for this paper because of the potential for a strong interaction between a decline in the numbers of individuals and reduced landscape connectivity.

This is again a good point and represents an interesting topic that we want to address in the future. Our justification for not doing this in the current work is that we are focussing on the targeted removal of diseased or damaged trees close to infrastructure in the event of a disease epidemic or climate induced dieback. Thus the loss of a percentage of trees from woodland is not relevant for this question. Again, we have added some text (L117, L396) to the manuscript to provide clarity on our choices in this current exercise, which really is focused on the impact of tree loss near infrastructure on wider landscape connectivity for actively dispersing woodland species.

Line 99-100: I disagree with the statement “trees outside woods (TOWs) seldom if ever are self-seeded.” In my opinion the dramatic decline in hedgerow management since 1945 has resulted in a huge increase in self-seeded ash, sycamore and hawthorn in hedges growing into adult trees. There are very large increases in TOWs over this period which cannot be attributed to planting.

With the restructuring of the introduction the above text has been removed and thus the above point addressed.

Lines 100-102: “Instead, they exist because they have been deliberately placed or at least allowed to persist.”…..in other words, planted or natural regeneration. I’m not sure if there are any other options, so this seems like a truism.

With the restructuring of the introduction the above text has been removed and thus the above point addressed.

“Unlike natural regeneration in woodlands, without human intervention the loss of TOWs marks a permanent decline in canopy.” I think that the authors are trying to say that in woodlands, canopy gaps are often rapidly filled. Trees lost from linear landscape features are much less likely to be replaced quickly.

With the restructuring of the introduction the above text has been removed and thus the above point addressed.

Lines 122-126: Text repeated at Lines 141-145.

This has been removed.

Lines 177-179: “Woodland patches were defined as the breeding habitat for the study species and other habitat types (roadside trees, matrix trees, matrix habitat) formed the inter-patch matrix each with a habitat-dependent movement cost associated.” I think, in this context, that “study species” is not *F. excelsior* but the 81 virtual species mentioned for the first time later on in this section. Please reword to avoid this confusion.

We have reworded this.

Line 343 they say that the numbers of roadside and lineside ash trees will run into billions – I think this is extremely unlikely, but in any case the authors quote the Tree Council figure of 27-60 million ash trees outside of woodlands in total, so they can't then have billions of roadside ash trees.

We have removed this sentence.

This paper is a useful demonstration of a modelling method but until more work has been done on the functional profiling of ash-using species it tells us little about the real-world impacts on ecological connectivity and appropriate mitigation strategies.

-Reviewer 3

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Tree disease impacts on ecological connectivity: developing models for assessment and mitigation strategies

Comments to authors

General comments

This paper aims to show the relevance of using a modeling approach to assess the impact of tree disease on functional connectivity. The idea of using connectivity modeling approaches to measure the importance of small landscape elements is interesting and fits in the scopes of the journal. My main concerns relate to the orientation of the paper toward tree disease, while for what I understand of the methods, the trees could fall because of disease, management or storm without changing the results. I understand that the question of the impacts of tree diseases in a hot topic, but it seems to me that the tree removal scenarios are not specific to the disease. By oriented the paper toward the "disease" aspect, I would have expected spatial pattern of tree removal related to the disease (for instance linked to the spreading of species or link to management choices in response to the disease). Here the removal of trees appears to be random. Such a random pattern may be relevant to represent the spatial spread of the disease, but in that case the point has to be done and justify in the text. Personally (and I have no idea of the epidemiology of the ash dieback, and such information should be given in the introduction/methods) I would have guess that the disease is spreading from a host to neighbors, creating clusters of falling trees (see discussion L345-350). The emphasis on the "disease" aspect is thus confusing, as the reader try to see how it's taken into account in the analyses, but can't find it. Generally, the logic

To summarize, it seems to me that the methods are adapted to answer the question of the relevance of modeling approach to assess the impact of tree removal, but not to answer the question of tree disease impact on connectivity, which would have imply combining another model to locate sick trees and ash dieback spread. I may be wrong, and some justification of the method underlying the scenarios may allow overcoming this problem. If I'm right, then I suggest rewriting the introduction (and related sections in the methods) to focus on the importance of trees as elements for connectivity, under different threats, diseases being one of them. Such change would enlarge the scope of the paper to "importance of trees for connectivity", which is relevant and interesting. It would also better fit with the points developed in the discussion.

Overall, he paper is mostly well written and pleasant to read. Early information about the taxa under study (insects) is missing for a good understanding.

Thank you. Following reviewer 3's suggestions we have reframed the manuscript to focus on the loss of roadside trees in response to more general threats than just ash dieback. Trees along infrastructure features such as roads, railways and watercourses occupy an increasing proportion of all trees outside of woodlands, but the impact of tree loss on wider landscape connectivity, due to felling in response to tree disease or climate induced dieback, remains unexplored. Thus the novelty of our study remains unchanged in that use a spatially explicit individual-based model to consider the impact of the loss of these trees on wider ecological landscape connectivity, as a first step towards understanding the most appropriate management and recovery response.

Specific comments

I have very few specific comments. The text is clear and well structured.

Title

See general comments. The paper does not explicitly study the impacts of tree disease, but rather the impact of tree loss. Similarly, the paper does not talk or develop scenarios about mitigation strategies, it's just a possible output (word) that appears in the title, abstract and conclusion. I would suggest to find a title oriented toward the

We have amended the title to 'Tree loss impacts on ecological connectivity: developing models for assessment'.

Abstract

See my general comments for the direction given to presentation of the study.

Context: it is unclear from this section that the focus is on animal connectivity favored by trees. I'm not sure of the interest of the "tree disease" focus; it could more simply be just tree loss (by disease or management choice). [AM1]

Objective: There is not true "response to ash dieback" (L19) taken into account in the study. Information about the taxons under study is missing: plants, animals, which ones?

Methods: The reference to Arcgis is not needed. The random selection for tree removal should be mentioned. I would like to have an idea of the of the 6 areas.

Conclusions: The reference to " mitigation strategies" is not supported by the study.

We have altered the abstract to reflect more accurately the direction of the study and the focus on tree loss and connectivity rather than tree disease.

Introduction

See my general comments. If the authors decide to keep the "disease" focus, then I find the introduction too general and not focused enough on the ash dieback. Some references to other diseases could be removed, while most of the information included in the "Study system" section should be given here. Information about the epidemiology of the disease is missing.

L122-126: That should appear before (maybe after L109?)

Similar to the abstract we have altered the introduction to reflect more accurately the direction of the study and the focus on tree loss and connectivity rather than tree disease.

Application

Study system

L129-141: Some of this should be included in the introduction (if the "disease focus" remains), to depict a better picture of the extent of the disease and give an idea of its potential impacts.

I miss here a description of (i) the natural mortality linked induced by ash dieback (and how long does it take for the tree to die) and (ii) information about how the disease spread. This information is important to understand the potential impacts and the management choices along roads. If the probability that a sick tree will contaminate neighbors is high, then fell large portions is necessary to stop the disease. If sick trees die within a year or two, then keeping them alive a little bit longer by deciding not to fell them will just preserve connectivity for these 2 years, but will have contributed to the spread of the disease. I think that this part needs to be partly rewritten to make the rational clearer, i.e. the justification of why sick trees shouldn't be cut.

L152-158: For me that belongs to the introduction

We have followed the advice of Reviewer 3 and reframed the manuscript to focus on tree loss and connectivity rather than ash dieback, this we have removed the study system section from the manuscript.

Data analysis

L244-245: What varied factors?

We have added the names of the factors (perceptual range, directional persistence, carrying capacity, matrix per step mortality risk).

Appendices

Please do not use acronyms in the tables, there is room here to facilitate the reading.

The acronyms have been replaced in appendix A, there is no sufficient space in the tables of appendix B to replace the acronyms.

[AM1]

Highlights

We model the removal of non-woodland roadside trees and the effects on wider landscape connectivity

Removing 60% of roadside trees decreased the number of successful dispersers by up to 17%

Trees outside of woodlands (TOWs) are important for maintaining landscape connectivity

Spatially explicit individual-based models are valuable tools for assessing the loss of TOWs

Tree loss impacts on ecological connectivity: developing models for assessment.

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Running heading: Modelling the impact of tree disease on ecological connectivity.

Key words: Connectivity, tree disease, tree mortality, modelling, RangeShifter, scattered trees, corridors

Abstract

Trees along linear features are important landscape features, and their loss threatens ecological connectivity. Until recently, trees outside of woodlands (TOWs) were largely unmapped however; the development of innovation mapping techniques provides opportunities to understand the distribution of such trees and to apply spatially explicit models to address the importance of trees for connectivity. In this study, we demonstrate the utility of models when investigating tree loss and impacts on connectivity. Specifically, we investigated the consequences of tree loss due to the removal of roadside trees, a common management response for diseased or damaged trees, on wider landscape functional connectivity. We simulated the loss of roadside trees within six focal areas of the south east of the UK. We used a spatially explicit individual-based modelling platform, RangeShifter, to model the movement of 81 hypothetical actively dispersing woodland breeding species across these agriculturally fragmented landscapes. We investigated the extent to which removal of trees, from roadsides within the wider landscape, affected the total number of successful dispersers in any given year and the number of breeding woodlands that became isolated through time. On average roadside trees accounted for less than 2% of land cover, but removing 60% of them (~1.2% of land cover) nevertheless decreased the number of successful dispersers by up to 17%. The impact was greatest when roadside trees represented a greater proportion of canopy cover. The study therefore demonstrates that models such as RangeShifter can provide valuable tools for assessing the consequences of losing trees outside of woodlands.

Introduction

The loss and fragmentation of habitats is a major threat to biodiversity (Haddad et al. 2015). Scattered trees within a fragmented landscape have a significant role to play in combating the effects of habitat loss and fragmentation. In a recent global meta-analysis, Prevedello et al. (2017) found landscapes with scattered trees supported greater levels of biodiversity than landscapes without scattered trees, reinforcing the idea that scattered trees are 'keystone' structures of landscapes (Fischer and Lindenmayer 2007; Gibbons et al. 2008). In particular, hedgerows and scattered trees alongside roads and railway lines are often cited as examples of habitat corridors (Bennett 1990; McCollin et al. 2000; Bailey 2007; Roy and de Blois 2008). Hedgerows and other linear tree features have been shown to aid the dispersal of some forest plants (Roy and de Blois 2008), pollen (Van Geert et al. 2010), mammals (De Lima and Gascon 1999; Laurance and Laurance 1999), birds (Fernandez-Juricic 2000) and insects (Petit and Burel 1998; Tischendorf et al. 1998). Trees present outside woodlands can also act as stepping stones, increasing connectivity and facilitating range expansion (Rossi et al. 2016). In a recent study, Fischer et al. (2010) found that scattered trees in an agricultural landscape had a disproportionately positive effect on species richness, thus emphasising their role as keystone structures in fragmented landscapes.

Many of these ecologically important landscape features are now under threat. Loss of scattered trees and connectivity is often associated with anthropogenic land use change, such as agricultural intensification and management. However, tree mortality rates and die-off events have increased greatly in some parts of the world as trees suffer from elevated temperatures and water stress due to climate change (Peñuelas et al. 2001; Breshears et al. 2005; Bigler et al. 2006; McDowell et al. 2010). Furthermore, in recent years, the number of tree diseases and their rate of spread appear to have increased across the globe, due to several factors including climate change and global trade (Woodward and Boa 2013). For example, in North America, chestnut blight *Cryphonectria parasitica* has caused near complete loss of chestnuts *Castanea dentata* (Jacobs 2007). Dutch elm disease *Ophiostoma* spp. has caused a similar loss of mature elms *Ulmus* spp. in Europe and North America (Potter et al. 2011): some 26 million landscape trees were lost in the UK alone during the major outbreak in the 1970s. Across Europe, ash *Fraxinus* spp. trees are also dying due to the ascomycete *Hymenoscyphus fraxineus* widely known as ash dieback (Kjær et al. 2012; Baral et al. 2014)(previously called *Chalara fraxinea* and *H. pseudoalbidus*). The impact of woodland tree loss due to threats such as deforestation, disease and climate change on biodiversity has been documented (Brook et al. 2003; Mitchell et al. 2014; Barlow et al. 2016). However, trees outside of woods (TOWs) are often overlooked and rarely mapped (see Levin et al. 2009; Gullick et al. 2017 as mapping exceptions). Yet the recent development of innovative high resolution mapping for mapping individual TOWs (Bluesky National Tree Map 2015) indicates that a large proportion of trees are present outside of existing mapped woodlands, thus the importance of TOWs for ecological connectivity may be undervalued. With the development of mapping techniques, opportunities to consider the value of TOWs for biodiversity and connectivity have arisen. In particular, the loss of TOWs, principally those close to infrastructure such as roads and railways, on wider landscape connectivity can be explored.

A suite of approaches already exists for modelling landscape ecological processes and new ones are emerging (Synes et al. 2016). Connectivity is one of the key attributes maintaining linkages between fragmented habitat patches within landscapes. Among the spatially explicit approaches for modelling connectivity are three distinctive methods, least-cost path (LCP) (Adriaensen et al., 2003), circuit theory (e.g. Circuitscape, McRae et al. 2008) and emerging mechanistic or process models, such as the stochastic movement simulator (SMS) which is embedded in the spatially explicit modelling platform RangeShifter (Palmer et al. 2011; Bocedi et al. 2014). Within all three, landscapes are characterised by habitat and matrix elements, each of which has a permeability or cost value associated with moving through it (related to the resistance/preference). The three approaches differ in the way they model the potential pathways individuals may use to travel between patches. At one extreme, LCP calculates a single, deterministic, optimum route between any two patches, whereas in Circuitscape (McRae et al. 2013) all possible pathways are evaluated by analogy to electrical resistance. SMS explicitly incorporates the movement behaviours of individuals, simulating the trajectories of many individuals making probabilistic decisions regarding each step evaluated within a limited perceptual range. In a recent study, the degree to which each estimator (LCP, Circuitscape and SMS) correlated with genetic estimates of connectivity was compared for an amphibian and a bird species having contrasting movement abilities: SMS was the best performer and Circuitscape outperformed LCP (Coulon et al. 2015). The improvement in performance gained by using SMS comes unavoidably with an increase in the number of parameters required for the model. However, embedding detailed individual movements into spatially explicit population models can offer important advantages over alternative methods for estimating connectivity (Coulon et al. 2015; Aben et al. 2016). Spatial modelling approaches have been used to estimate ecological connectivity and to inform landscape management options in other contexts (Binzenhöfer et al. 2005; Conlisk et al. 2014; Synes et al. 2015; Aben et al. 2016). Yet, there is considerable untapped potential to develop and apply spatially explicit models, incorporating mechanistic dispersal, to address landscape connectivity questions related to the impact of climate change, tree disease and/or management actions that lead to the loss of scattered trees outside of woodlands.

In this study, we construct a spatially explicit individual-based model for actively dispersed virtual species that are assumed to use roadside trees as stepping stones and/or corridors between woodland breeding habitats in real UK landscapes. We use the recently developed innovative high resolution national tree map for mapping individual TOWs (Bluesky National Tree Map 2015). In an intensively managed landscape such as the UK, TOWs are often an important ecological component within the highly fragmented and hostile agricultural matrix. As field sizes have expanded with the intensification of agriculture, trees along infrastructure features such as roads, railways and watercourses have occupied an increasing proportion of all TOWs. However, infrastructure brings people into contact with such trees and concerns over perceived danger presented by diseased or dying trees (i.e. their inherent tendency to limb failure or collapse) increases the likelihood of management actions targeting the removal of trees close to infrastructure in the event of a disease epidemic or climate-induced dieback (Gullick et al. 2017). We aim to consider the impact of this manner of tree loss on wider ecological landscape connectivity, as a first step towards understanding the most appropriate management and recovery response. Specifically, we model actively dispersing woodland breeding species, and investigate the extent to which the removal of roadside trees affects the total number of successful dispersers in any given year and the number of breeding patches that become isolated through time. We present results demonstrating the utility of individual-based spatial models, incorporating mechanistic dispersal, for addressing questions related to connectivity and tree loss, and discuss the potential of modelling to inform applied management.

Methods

Study landscapes

Our study landscapes consisted of six 10km x 10km squares in the south east of the UK (Table 1, Figure 1). This region is a good example of an area with trees under threat; ash dieback is prevalent within the region and is expected to cause the catastrophic loss of ash trees that comprise a substantial proportion of all trees in the wider landscape. Furthermore, climate change and subsequent increasing heat and drought in the south and east of the UK are also likely to increase tree loss, particularly of young trees and mature trees outside of woodlands (Broadmeadow et al. 2009).

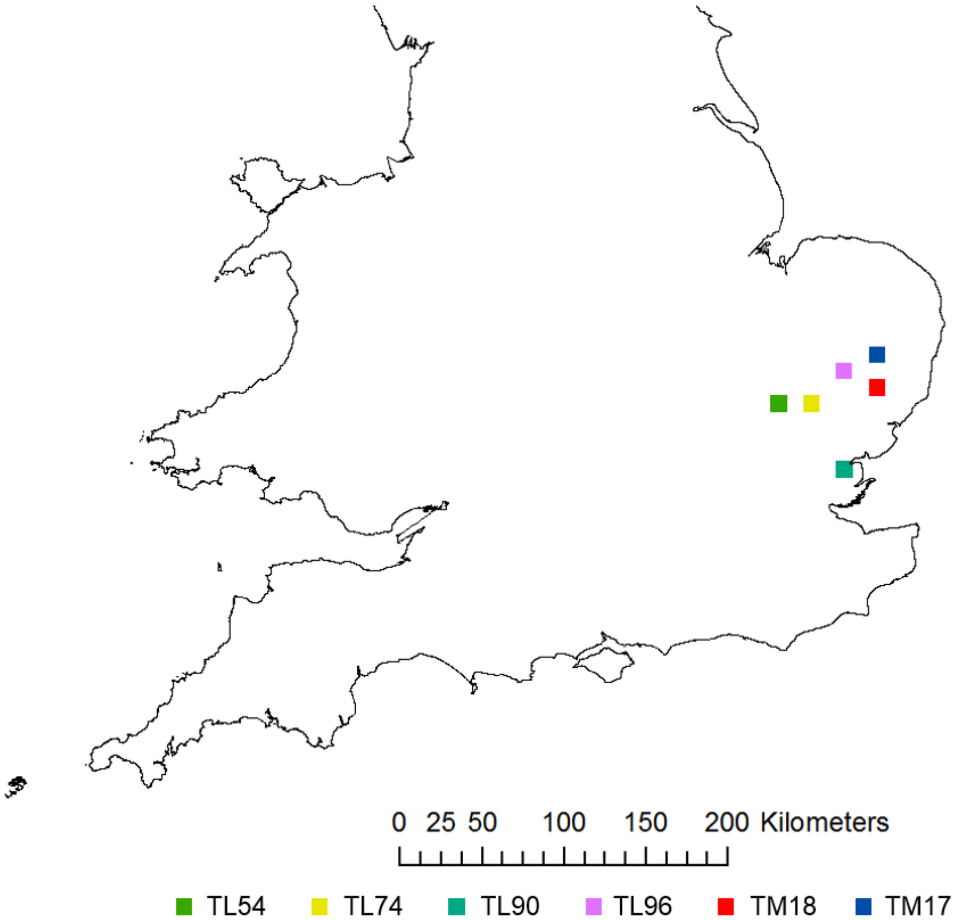

Figure 1: Map of southern England showing square locations.

Square	SW corner co-ordinates (°Lat,°Lon)	Tree cover (%)			
		Total	Matrix	Roadside	Woodland
TM18	52.108, 1.065	13.3	6.4 (48.3)	2.2 (16.3)	4.7 (35.4)
TL96	52.205, 0.779	15.7	5.6 (35.8)	2.4 (15.5)	7.6 (48.7)
TL54	52.038, 0.185	14.2	5.6 (39.2)	2.0 (14.4)	6.6 (46.4)
TM17	52.288, 1.078	12.1	5.8 (47.6)	2.1 (17.7)	4.2 (34.7)
TL74	52.032, 0.477	10.3	5.0 (49.1)	1.7 (16.9)	3.5 (34.0)
TL90	51.667, 0.746	6.1	3.5 (58.2)	1.4 (22.4)	1.2 (19.4)

Table 1: Tree cover as a percentage of land cover within each of the 10km x 10km study squares, and in parentheses the percentage of the total tree cover for the three classes, matrix, roadside and woodland trees.

The squares were selected to provide a representative range of landscapes in the region. Baseline maps were created using canopy tree data extracted from the National Canopy Map (NCM) for England and Wales provided by BlueSky (Bluesky National Tree Map 2015) under licence to the Woodland Trust. The NCM provides the location, height and canopy/crown extents where canopy exceeds 3m in height. It is created from high resolution aerial photography, terrain and surface data, and from colour/infrared satellite imagery. Using ArcGIS, NCM tree cells were classified as woodland trees if they fell within the Forestry Commission's National Forest Inventory (National Forest Inventory Great Britain 2015) woodland polygons of >0.5 ha extended by a buffer of 10m width. Road data for the study area were downloaded from Edina (http://digimap.edina.ac.uk) OS open roads. Linear road features were buffered to 25m either side and tree cells were classified as roadside trees if they fell within the road buffer. Matrix trees were those that did not fall within the boundaries of NFI woodlands or road buffers. The remainder of the landscape was dominated by agricultural land classified within our model as hostile matrix habitat. Woodland patches were defined as the breeding habitat for the 81 virtual species (described below), and other habitat types (roadside trees, matrix trees, matrix habitat) formed the inter-patch matrix (Figure 2) each with a habitat-dependent movement cost associated (Table 2). Thus, we restricted the models to species that need a woodland patch for reproduction. For these species, the trees outside of woodland improve the permeability of the matrix. We have not focused on species for which single trees outside of woodland provide suitable breeding habitat. 10m raster maps were then created from the ArcGIS shapefile layers with cells identified as woodland trees, roadside trees, matrix trees and inter-patch matrix (Figure 2a).The percent of the tree cover for each square and the composition of the tree cover (matrix, road side, or woodland trees) is given in Table 1.

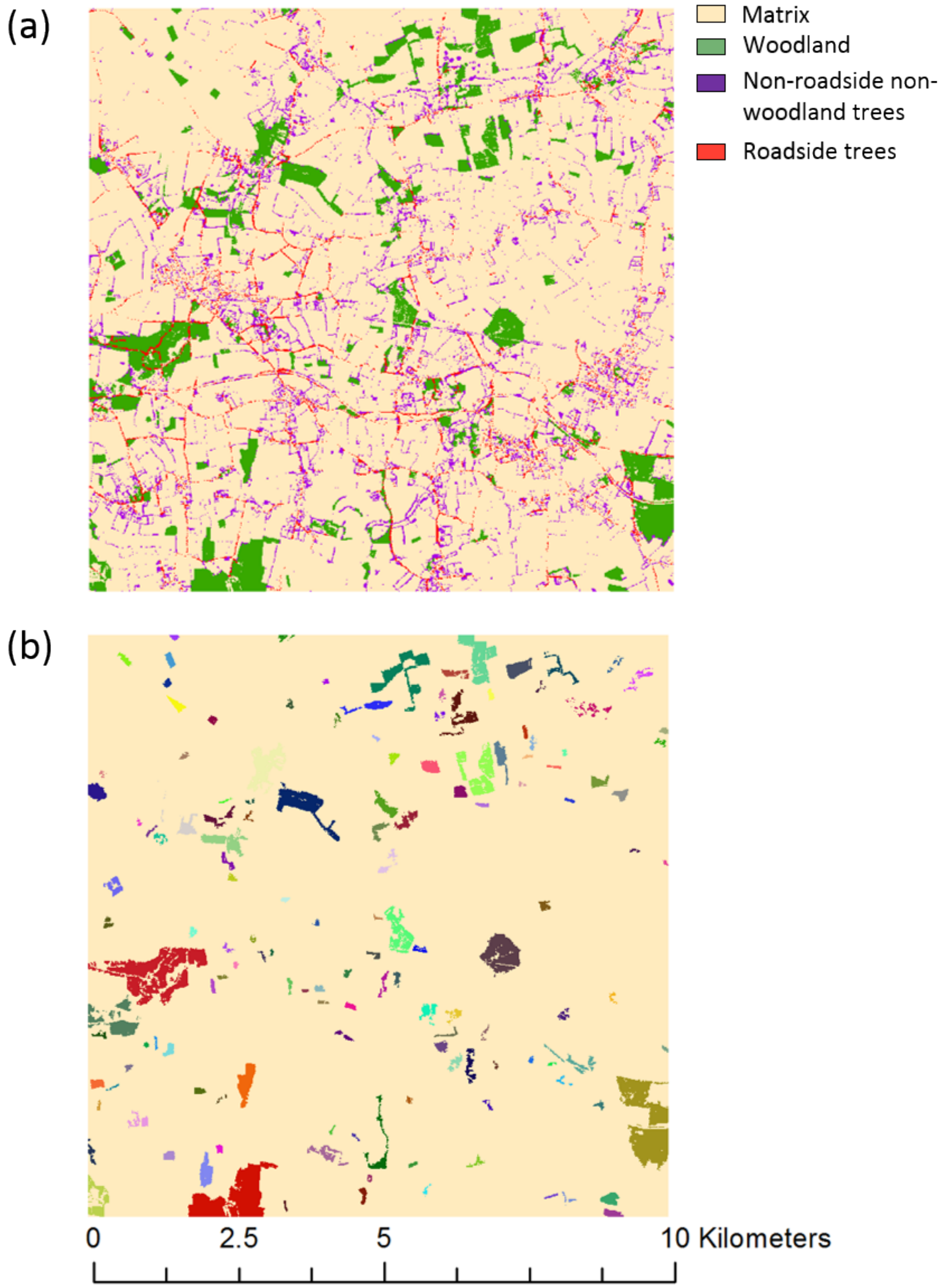

Figure 2: Example of one of the six landscape squares (TL96) showing (a) the classification into four habitat types and (b) the 144 discrete breeding patches in the square (unique colours).

Tree removal scenarios

We simulated the removal of 20%, 40% and 60% of roadside trees in each square due to anticipated felling of diseased and damaged trees along roads. For each of the six squares and for each of the 20%, 40% and 60% removal scenarios, we generated ten landscape replicates in which roadside trees were removed at random from the baseline landscape (for an example of this see Figure 3). Thus for each of the six squares, breeding patches remained the same in the baseline landscape and in each of the 30 generated removal landscape replicates, but the inter-patch matrix differed.

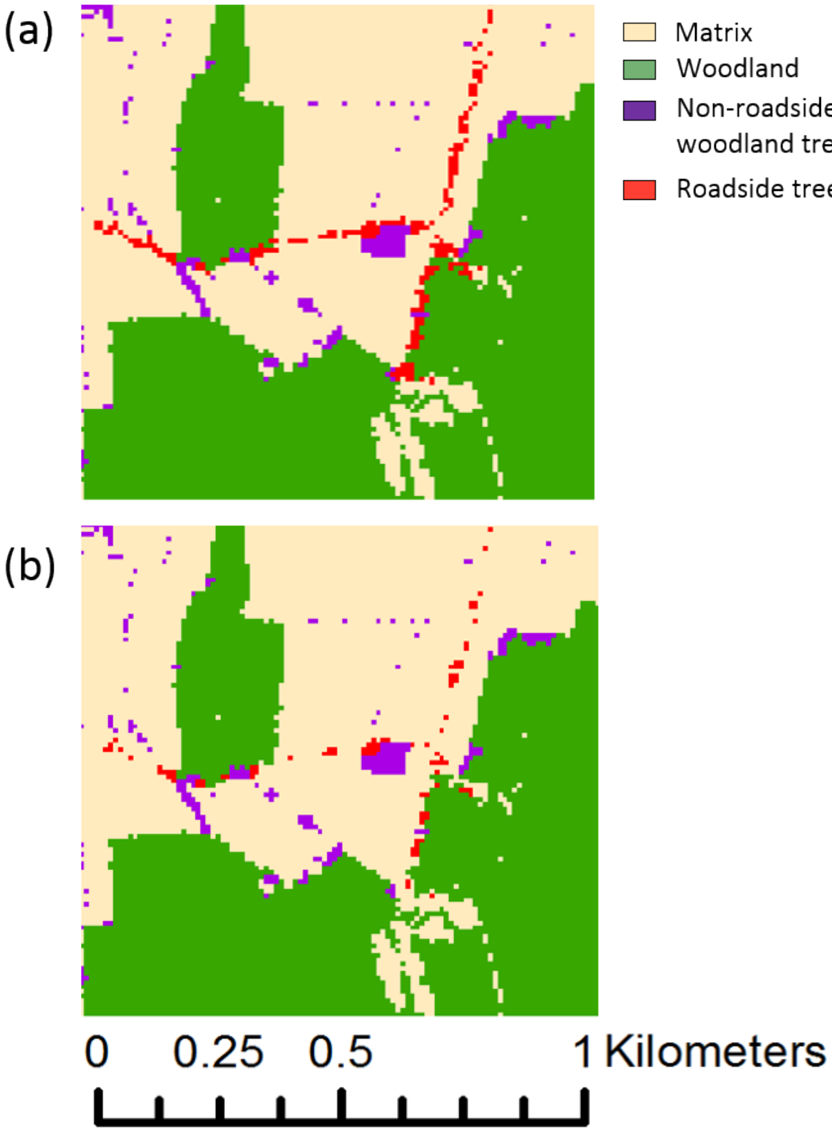

Figure 3: (a) Example of a 1km x 1km area within one of the six landscape squares (TL96) (b) Example of 60% roadside tree removal for the area shown in (a).

Model

We modelled the effects of the tree removal scenarios on connectivity using RangeShifter, an individual-based spatially explicit modelling platform (Bocedi et al. 2014), which combines demographic and dispersal sub-models, notably accounting explicitly for the three phases of dispersal (emigration, transfer, settlement). Within RangeShifter, the distribution of individuals' dispersal distances is an emergent property of behavioural rules at each phase and interaction with the landscape (e.g. the dispersal of an individual between two woodland patches depends upon the quality of the matrix). For the purpose of this study, the movement of individuals was modelled using SMS, which is embedded within Rangeshifter. SMS simulates the movement of individuals between breeding sites across a cost surface, subject to two key movement parameters, namely perceptual range (*PR*, the distance within which an individual evaluates surrounding habitat costs) and directional persistence (*DP*, an individual's predisposition to follow a correlated path). In addition to matrix cells having a substantially higher movement cost than cells with trees, they also had a much higher mortality risk in terms of the habitat-dependent risk of mortality per step taken.

Simulations

For each of the landscapes, we simulated the dynamics of virtual species. The use of virtual species in spatial ecological modelling is increasing used (Fukuda and De Baets 2016; Feng and Papeş 2017) and presents advantages in terms of facilitating the development, testing and showcasing of methods (e.g. Leroy et al. 2016). Furthermore it can provide initial insights on potential impacts of environmental changes and management activities even when data are lacking for sets of real species (e.g. Saura et al. 2011; Synes et al. 2015). We considered actively dispersing species that might use roadside trees as stepping stones and/or corridors for movement between woodlands. We assumed that such species would have sensory abilities to navigate towards trees in the landscape, and would display a strong preference for doing so rather than moving across open fields. A list of species within the study area and their associated demographic and dispersal parameters was not available; thus the set of model species is not based on particular species, but has been designed to represent the characteristics of a broad range of potential invertebrate taxa, varying in their population densities and dispersal abilities.

The virtual species were modelled as asexual with non-overlapping generations. The choice to model asexual populations does not imply only asexual reproduction, but rather represents invertebrate species that mate prior to emigrating from their natal patch; hence new colonies are founded by fertilised females and the dispersal of males does not need to be modelled. The 81 species were chosen using a fully factorial design by applying three levels of each of the following parameters: carrying capacity (*K* = 25, 50, 75 inds/ha), perceptual range (*PR* = 3, 6, 12 cells), directional persistence (*DP* = 5.0, 7.0, 9.0) and the mortality risk incurred by crossing unsuitable matrix habitat (*HM* = 0.02, 0.035, 0.05). Other parameters within RangeShifter were held constant for all simulations (Table 2).

For each of the 81 species, 10 demographic replicate scenarios were run on the baseline landscapes to generate baseline measures of connectivity. Then, for each species, 10 demographic replicates were run on each of the 30 removal scenario landscapes for each of the six squares (10 replicate landscapes for each of the 20%, 40% and 60% roadside tree removal scenarios). For each species, landscape and replicate combination, populations were initialised at half carrying capacity in every breeding patch. The models ran for 30 years, but the first 10 years were taken as a burn-in period and discarded, as trial simulations had demonstrated that this allowed for the population dynamics to stabilise before results were taken.

Demographic Parameter	
Reproduction	Asexual / female only
Stage structure	Non-overlapping generations
Intrinsic growth rate (*Rmax*)	10
Competition coefficient (b_c)	1
Carrying capacity (inds/ha) (*K*)	25, 50, 75
Dispersal Characteristics	
Emigration probability	Density-dependent
Max. emigration probability (D_0)	0.7
Slope at inflection point (α)	10
Inflection point (β)	0.5
Movement model	SMS
Perceptual range (cells)	3,6,12
Perceptual range method (*PR*)	Harmonic mean
Directional persistence (*DP*)	5.0,7.0,9.0
Memory size (cells)	2
Maximum number of steps (cells)	2000
Cost value / mortality risk (*HM*) of:	
Matrix	500 / 0.02, 750 / 0.035, 1000 / 0.05
Woodland	1 / 0.0001
Matrix trees	1 / 0.0001
Roadside trees	1 / 0.0001
Settle-if	Find a suitable patch (not the natal one)

Table 2: Parameters used in RangeShifter, varied parameters shown in red.

Data analysis

For each generation, RangeShifter provides a connectivity matrix presenting counts of the number of successful dispersers from each breeding patch to every other breeding patch in the study area. The connectivity matrices were used to calculate the total number of successful dispersers (individuals that did not die during dispersal) in any given year and the number of breeding patches that become isolated (patches receiving no immigrants in the 20 years after the burn-in period).

Baseline landscapes

General linear models were fitted in R using package lme4 (Bates et al. 2015; R Team 2017) to apportion the variance explained by each of the four varied factors (perceptual range, directional persistence, carrying capacity, matrix per step mortality risk). For all squares, demographic replicate and year, together with their interactions with the four varied factors, accounted for < 0.01% of the variance in the number of successful dispersers (Appendix A, Table A1) and in the number of isolated patches (Appendix A, Table A2). Therefore, counts of successful dispersers and the number of isolated patches were averaged across all demographic replicates and years.

Removal scenarios

For all tree removal scenarios (20%, 40%, 60%) on all squares, demographic replicate and year, together with their interactions with the four varied factors, accounted for < 0.01% of the variance in the number of successful dispersers (Appendix A, Tables A3,A4,A5). Therefore, as with the baseline, the number of successful dispersers was averaged across all demographic replicates and years for each landscape replicate within a given square and removal scenario. The mean number of successful dispersers was then scaled as a proportion of the baseline mean for the corresponding simulation (i.e. combination of *K*, *HM*, *PR* and *DP*).

Similarly, the number of isolated patches was averaged across all demographic replicates and years, and the effect of tree removal was represented by the increase in the mean number of isolated patches relative to the corresponding baseline simulation.

To account for all species simulations being run on the same 10 landscapes replicates (LR) for a given removal scenario in a particular square, the data were fitted separately for each square to linear mixed models in which landscape replicate was included as a random effect. The least squared means for the four varied factors (*K*, *HM*, *PR*, *DP*) were extracted from these models using R package lsmeans (Lenth 2016) to illustrate the main effects of each model parameter.

Results

Successful dispersers

For each square, the mean proportion of successful dispersers declined as the percent of trees removed increased (Table 3). In general, the reduction in successful dispersers due to tree removal was less than 10%, but for some individual parameter and landscape replicate combinations, the reduction in successful dispersers could be up to 17%. Removing roadside trees also changed the dispersal trajectories of individuals and increased the frequency of disperser visits to cells containing non-roadside matrix trees (Figure 4).

					Proportion of variance explained by				
Square	**% of trees removed**	**Mean**	**Min**	**Max**	**LR**	**PR**	**DP**	**K**	**HM**
TM18	20	0.979	0.964	0.991	**0.210**	0.023	0.063	0.090	0.128
TM18	40	0.959	0.934	0.979	**0.202**	0.013	0.090	**0.321**	0.088
TM18	60	0.941	0.913	0.967	0.030	0.015	0.151	**0.427**	0.064
TL96	20	0.979	0.953	0.994	0.166	0.048	0.107	**0.274**	0.038
TL96	40	0.959	0.926	0.984	0.081	0.084	0.147	0.344	0.096
TL96	60	0.941	0.896	0.973	0.086	0.077	0.157	0.302	0.148
TL54	20	0.979	0.965	0.992	0.124	0.025	0.123	0.185	0.197
TL54	40	0.959	0.933	0.981	0.077	0.042	0.162	**0.254**	**0.230**
TL54	60	0.938	0.900	0.967	0.052	0.037	0.182	**0.282**	**0.253**
TM17	20	0.979	0.954	0.999	0.163	0.051	0.111	**0.212**	0.068
TM17	40	0.959	0.925	0.989	0.045	0.038	0.158	**0.381**	0.064
TM17	60	0.940	0.901	0.977	0.040	0.028	0.139	**0.496**	0.019
TL74	20	0.982	0.959	1.003	0.141	0.024	0.083	**0.277**	0.017
TL74	40	0.967	0.936	0.996	0.048	0.026	0.110	**0.408**	0.052
TL74	60	0.952	0.909	0.984	0.063	0.023	0.084	**0.496**	0.032
TL90	20	0.974	0.940	1.018	0.178	0.015	0.001	0.045	0.068
TL90	40	0.944	0.897	0.983	0.102	0.033	0.011	**0.336**	0.062
TL90	60	0.916	0.832	0.962	**0.302**	0.029	0.009	**0.280**	0.025

Table 3: Mean, minimum and maximum proportion of successful dispersers relative to the baseline landscape for each tree removal scenario on each square and the proportion of variance explained by the main model parameters LR (landscape replicate). PR (perceptual range). DP (directional persistence). K (carrying capacity). HM (matrix per step mortality risk) . Values >0.2 are highlighted in bold.

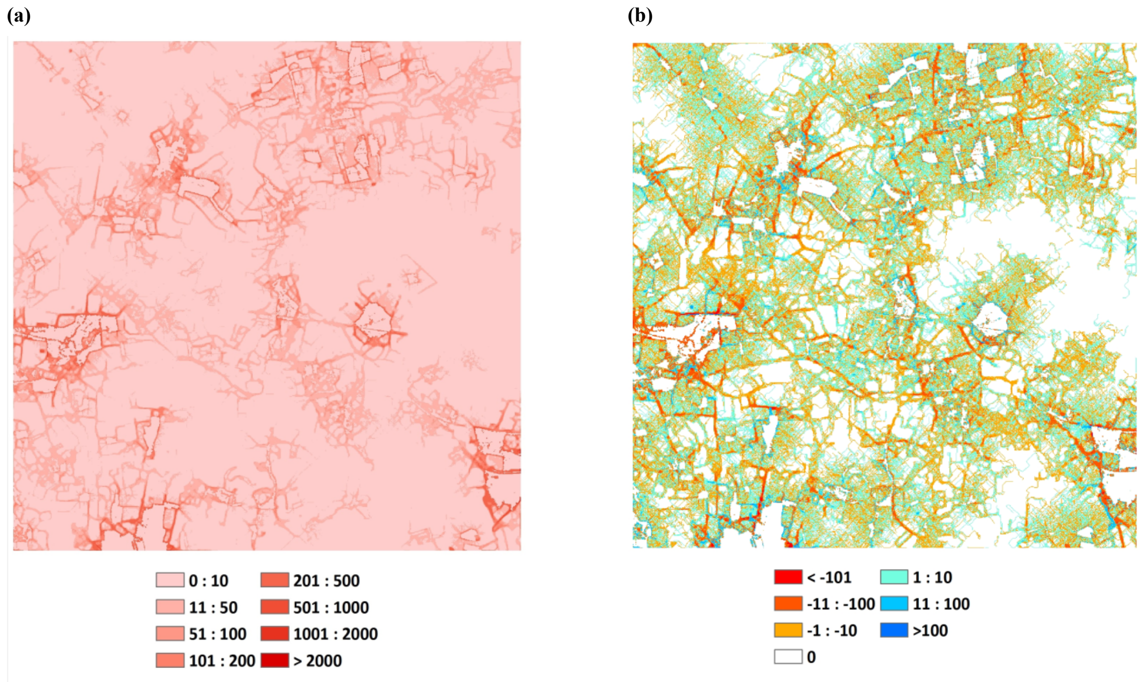

Figure 4. Examples of (a) the number of times each cell of the baseline landscape of square TL96 was traversed by a dispersing individual during the course of 20 years and (b) the change in visit frequency for a single landscape replicate following removal of 60% of the roadside trees (red – fewer visits; blue – more visits). RangeShifter parameter values were as shown in Table 2, varied parameters being set to their intermediate values.

The proportion of variance in successful dispersers explained by landscape replicate was between 3% and 30%, indicating that the actual spatial pattern of tree removal is likely to be important for connectivity. As the percent of trees removed increased, the proportion of variance explained by landscape replicate (LR) decreased (TL90 was the exception). Thus, in general as more trees were removed the spatial pattern of tree removal becomes less important. Conversely, as more trees were removed the variance explained by carrying capacity (K) and directional persistence (DP) increased and the proportion of variance explained ranged from 5% to 50% and <1% to 18% respectively. The interaction of carrying capacity and per-step mortality risk accounted for between 0.7% and 12% of the variance, but otherwise interactions were relatively unimportant.

Increasing carrying capacity (K) and matrix per step mortality risk (HM) (Figure 5a and 5b, appendix B table B1) decreased the mean proportion of successful dispersers. Conversely, increasing SMS directional persistence (DP) increased the mean proportion of successful dispersers (Figure 5c, appendix B table B1).

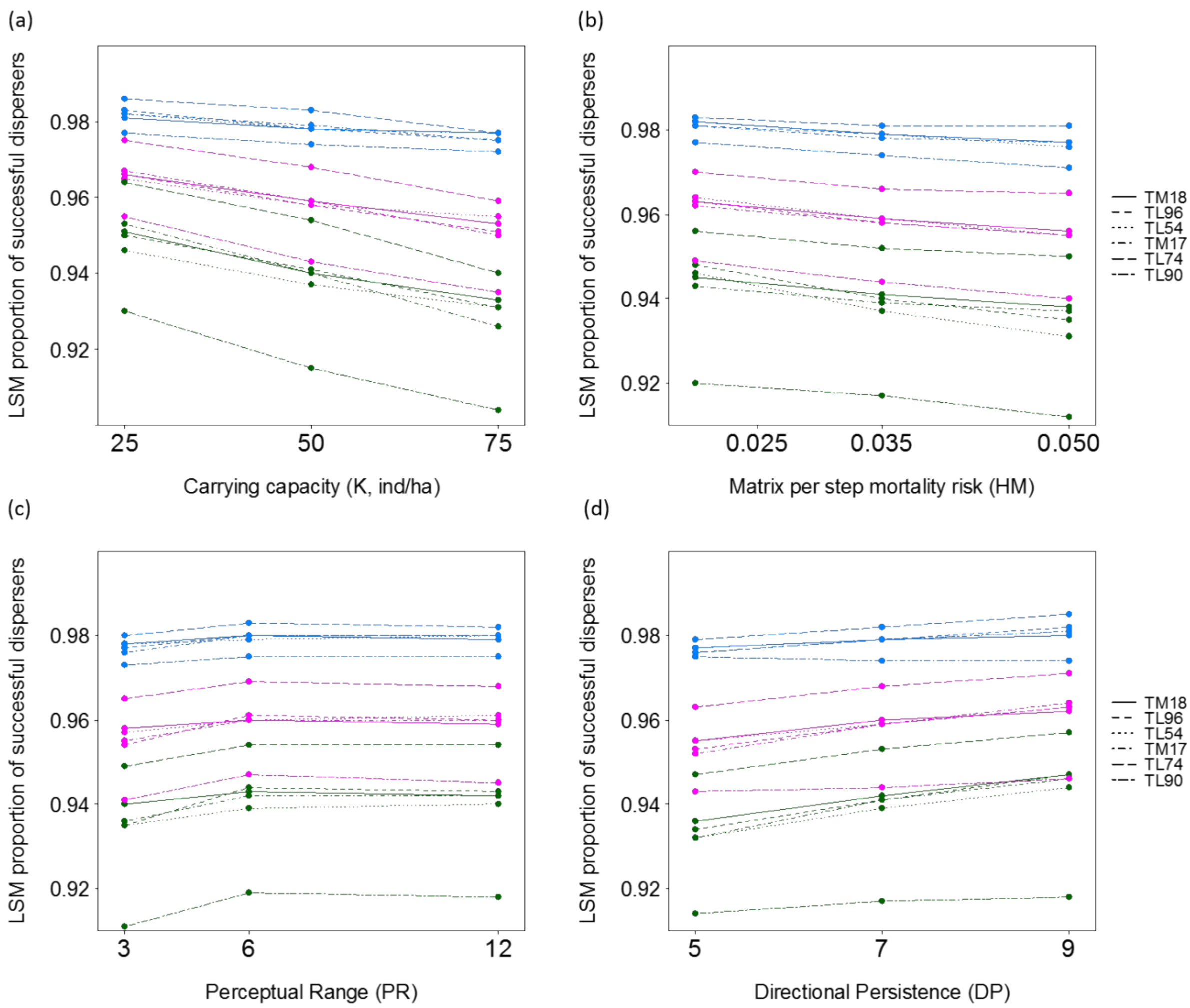

Figure 5: Least squares mean proportion of successful dispersers illustrating the effect of carrying capacity (a), matrix per step mortality risk (b), SMS perceptual range (c), and SMS directional persistence (d) in the 20% (blue), 40%(pink) and 60%(green) removal scenarios for each square. For each factor of interest, results were averaged over the levels of the remaining factors.

Isolated patches

At only 20% roadside tree removal, the increase in patch isolation over baseline levels was very limited, but larger increases in isolation were observed at higher levels of removal (Table 4, Figure 6). Overall, the mean change was limited because some spatial configurations allow for a more substantial decrease and some an increase in patch isolation. For example, in the worst-case scenario the maximum increase in the number of isolated patches was 3.9 above the baseline (Table 4). However, in some cases tree removal also decreased the number of isolated patches compared to the baseline, minimum values ranging between -1.2 and -2.1 (Table 4). Increasing the per-step mortality risk led to larger increases in the number of isolated patches, whereas increasing directional persistence resulted in smaller increases (Appendix B Table B2, Figure 6). Main effects and their first-order interactions generally accounted for a small proportion of the variance in the isolation metric, although the influence of mortality risk and directional persistence increased considerably as the proportion of trees removed increased.

					Proportion of variance explained by				
Square	% of trees removed	Mean	Min	Max	LR	PR	DP	K	HM
TM18	20	0.148	-1.9	2.6	0.019	0.000	0.017	0.023	0.020
TM18	40	0.383	-1.3	3.4	0.016	0.001	0.072	0.031	0.092
TM18	60	0.501	-1.2	2.8	0.034	0.003	0.085	0.016	0.126
TL96	20	0.223	-1.9	3.2	0.026	0.024	0.029	0.006	0.066
TL96	40	0.450	-1.4	3.4	0.034	0.007	0.161	0.011	0.152
TL96	60	0.531	-1.4	3.9	0.027	0.018	0.165	0.011	0.198
TL54	20	-0.036	-1.9	1.2	0.013	0.013	0.042	0.012	0.001
TL54	40	-0.037	-1.4	1.7	0.020	0.009	0.046	0.008	0.007
TL54	60	0.011	-1.6	1.9	0.055	0.009	0.018	0.009	0.081
TM17	20	0.228	-2.1	2.7	0.015	0.007	0.062	0.015	0.042
TM17	40	0.366	-1.3	2.9	0.014	0.003	0.120	0.001	0.096
TM17	60	0.596	-1.2	3.1	0.027	0.003	0.147	0.002	0.132
TL74	20	0.023	-2.1	1.9	0.009	0.000	0.001	0.005	0.009
TL74	40	0.075	-1.9	2.4	0.008	0.000	0.001	0.022	0.006
TL74	60	0.034	-1.7	2.6	0.012	0.000	0.015	0.010	0.011
TL90	20	0.160	-1.6	1.9	0.012	0.032	0.003	0.001	0.055
TL90	40	0.404	-1.3	2.3	0.009	0.021	0.029	0.009	0.167
TL90	60	0.610	-1.2	3.1	0.017	0.007	0.050	0.013	**0.256**

Table 4: Mean, minimum and maximum increase in the number isolated patches relative to the baseline landscape and the proportion of variance explained by the main model parameters LR (Landscape Replicate), PR (perceptual range), DP (directional persistence), K (carrying capacity), HM (matrix per step mortality risk) . Values >0.2 are highlighted in bold.

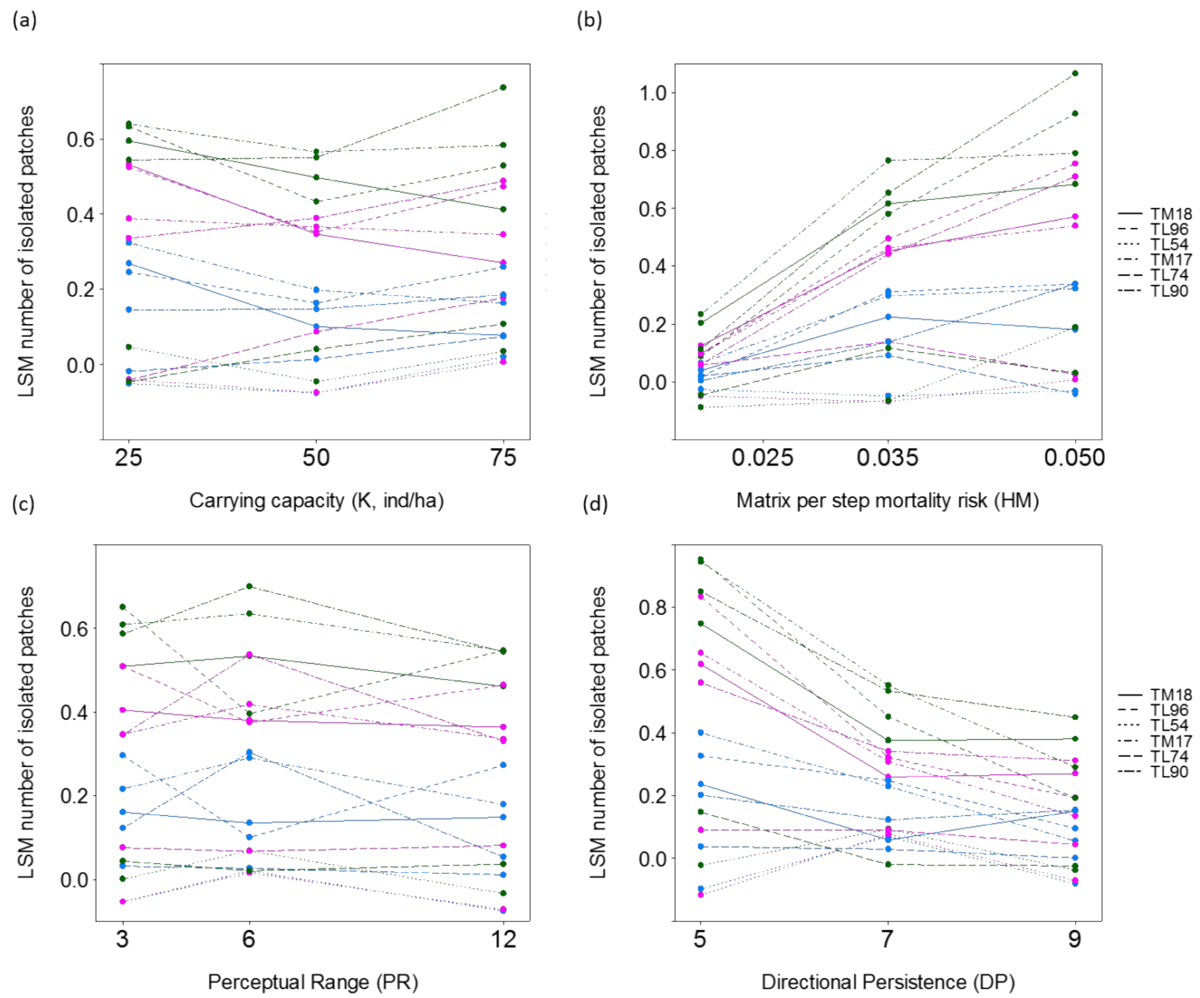

Figure 6: Least squares mean change in the number of isolated patches illustrating the effect of carrying capacity (a), matrix per step mortality risk (b), SMS perceptual range (c), and SMS directional persistence (d) in the 20% (blue), 40%(pink) and 60%(green) removal scenarios for each square. For each factor of interest, results were averaged over the levels of the remaining factors.

Discussion

Here, we have demonstrated a novel approach for modelling how the removal of TOWs can affect the connectivity between woodlands in a fragmented landscape. A number of approaches have been used to assess and model landscape connectivity, ranging from simple pattern based metrics (e.g. nearest neighbour), to more complex techniques to model potential connectivity (e.g. graph theory) and the use of individual-based models to capture the process of dispersal (Calabrese and Fagan 2004). We demonstrate that using a spatially explicit individual-based model provides advantages over other approaches, as it allows for greater detail in the dispersal process so that inter-patch dispersal rates become an outcome of context and behaviour-dependent dispersal decisions rather than deterministic connectivity metrics or a fixed distribution (O'Brien et al. 2006; Saura et al. 2011). Using RangeShifter, there were clear indications that the removal of roadside trees would lead to loss of connectivity in our case study landscapes. While roadside trees accounted for less than 2% of land cover, removing 60% of these roadside trees (~1.2% of land cover) nevertheless decreased the number of successful dispersers by up to 17%. For some species, this could represent substantial degradation to ecological and/or genetic function. The impact of removing roadside trees on dispersal success was greatest where these trees represented a greater proportion of total canopy cover in the landscape. The effect of roadside tree removal on the mean proportional reduction in the total number of successful dispersers per year was roughly linear, i.e. for each successive 20% of trees removed; there was a consistent reduction relative to the baseline.

The relative proportion of successful dispersers decreased slightly with increasing carrying capacity and per-step mortality risk but increased slightly with increasing directional persistence and perceptual range, although in all cases there was less than a 10% change compared with the baseline landscape. At higher levels of tree removal, the modelled species suffering greater risk when crossing open terrain were likely to experience the greatest reduction in connectivity, whereas species with better sensory abilities and those that tended to move more directly through the landscape, regardless of tree availability, were to some extent able to compensate during dispersal. In a recent study of connectivity in European forests, using a network based approach with theoretical species, results similarly indicated that more mobile species would be better able to cope with changing spatial forest patterns and increasing forest cover increased connectivity overall (Saura et al. 2011).

The effect of roadside tree removal on patch isolation was more complex than its effect on overall disperser success. In most cases, roadside tree removal resulted in increased patch isolation; both empirical and theoretical studies have similarly found that maintaining habitat between breeding patches reduces the risk of patch isolation and is also important for facilitating range expansion (Roy and de Blois 2008; Conlisk et al. 2014; Saura et al. 2014; Aben et al. 2016; Rossi et al. 2016). However, in some simulations individual patches became better connected when roadside trees were removed. An explanation for this result is that some roadside trees made certain pairs of patches well connected, and thus their removal encouraged dispersers away from those patches and into patches that would have otherwise remained poorly connected. Effectively, in the baseline, some of the non-woodland trees acted to direct dispersers in particular directions and away from routes linking patches that are less attractive due to an absence of non-woodland trees on route. A similar dichotomous result arose in a modelling study of the European Lynx (*Lynx lynx*) (Kramer-Schadt et al. 2011). The introduction of stepping stones had a positive effect on lynx populations but in some cases could also distract dispersers from more suitable breeding habitat patches. Such contrasting potential outcomes indicate that conservation planning needs to consider trade-offs that may arise when considering the functional connectivity of landscapes (Kramer-Schadt et al. 2011).

The squares used in the study all had similar proportions of trees. Furthermore, tree cover only accounted for <16% of the landscapes, this being typical of many UK landscapes, and the proportion of roadside trees accounted for on average 17.2% of canopy cover. Our results highlight that the loss of a small proportion of trees can have a substantial impact on connectivity, but on our case study landscapes the non-roadside matrix trees may have somewhat buffered the loss of roadside trees. In the worst case, for 60% tree removal in square TL90, the number of successful dispersers was reduced to 83% of its mean in the baseline landscape. TL90 had the lowest tree cover of all the squares, and a smaller proportion of woodland trees, whereas roadside trees accounted for a greater proportion of trees than in other squares. In the current study, we chose to investigate the targeted removal of trees close to infrastructure, and did not model the loss of matrix trees or woodland trees that may occur due to increasing natural mortality caused by disease outbreaks and/or climate change. Furthermore, while we model the loss of up to 60% of roadside trees, the true extent future road- and rail-side trees loss is uncertain and it could be greater. Thus, the combined loss of roadside, matrix and woodland trees due to the combined effect of felling and natural mortality may lead to greater losses in connectivity.

In this study, we made simplifying assumptions about the spatial patterns of tree removal; roadside trees were randomly removed. However, it may be that trees will be felled in spatially aggregated patches for a number of reasons. For example, individuals of the same species may tend to be clustered and thus, depending on disease epidemiology, clusters may need be felled if all become diseased. Furthermore, when a dying tree is identified along a roadside, it is economically more efficient to remove all potentially dangerous roadside trees in close proximity at the same time. In our study, between 3 and 30% of the variance in the proportion of successful dispersers was explained by landscape replicate, and therefore the location of tree removal was clearly important. An interesting extension of this study would be to investigate explicitly the spatial pattern of tree removal. In particular, when tree loss is driven by tree disease, combining models of disease spread (Gilligan and Van Den Bosch 2008; Meentemeyer et al. 2011; Potter et al. 2011) with models describing human decision making in terms of tree felling (Gullick et al. 2017) could predict realistic patterns of tree loss, and connectivity estimates would be a novel application. Moreover, although our selected squares reflected a range of canopy coverage typical of an area of the South East of the UK, the scope of this initial limited study was such that inferences for individual UK counties or for the wider UK landscape cannot be drawn. Future work should randomly sample a greater number of locations from across counties of interest or indeed, across the UK, to draw county/country level conclusions. Nevertheless, results here demonstrate the utility of modelling approaches for addressing pressing landscape ecological questions.

We considered only the impact of tree loss on connectivity, but spatially explicit population models could also be used to investigate the impact of tree loss and the loss of linear woody features on the genetic health of populations. Indeed, Athayde et al. (2015) found that scattered trees held between 64-85% of the total functional and phylogenetic diversity in agricultural landscapes, and functional and phylogenetic diversity levels were higher in agricultural landscapes with scattered trees than expected for random assemblages of species. The use of models can also be extended to investigate mitigation options for tree disease. For example, Gibbons et al. (2008) used a model to explore management options to mitigate the decline of scattered trees in an agricultural landscape, identifying key variables that can be manipulated to reduce the impact. In terms of connectivity, modelling efforts investigating the costs/benefits of alternative management strategies, such as maintaining selected ecologically important trees to maintain ecological connectivity, would be a worthy future step. There is clearly much scope for models to address key ecological and management questions related to tree loss, particularly if models can be parameterised to reflect local conditions.

In general, while the model here was parameterised to represent a range of dispersers, if none of the actual species present in the study area possesses any of the factor combinations leading to poor dispersal, then it is possible that there would be no decline in connectivity. Alternatively, if such combinations of factors are common in real species, then the decline may be much more severe than predicted. Ultimately, better dispersers may be less affected by tree loss, while highly sensitive species, suffering higher mortality risks when crossing hostile habitat, may fare poorly in landscapes without scattered trees (Prevedello et al. 2017). Virtual species explorations such as those presented here provide valuable general insights; however, for most studies, ours included, there remain insufficient data to parameterise models for multiple species of interest (Saura et al. 2011). Yet this modelling framework could yield more robust management recommendations, for maintaining connectivity, when combined with high quality field-based estimation of parameters and/or a trait space approach (Aben et al. 2016; Santini et al. 2016). Furthermore, by identifying factors that make species vulnerable to tree loss, this type of virtual study could be used as an early indicator of risk for species found to possess those traits. Increasing and maintaining landscape connectivity is widely recognised as an essential component of biodiversity conservation, preventing population declines and facilitating adaptation to climate change. TOWs are vital landscape components that maintain connectivity and their loss, not only in areas close to infrastructure but also in the wider landscape, threatens ecosystems. There is clearly a pressing need to combine models of realistic tree loss with real species data quantifying traits, to ensure that future conservation actions are based upon robust evidence to deliver real biodiversity benefits.

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Appendix A

Factor	Square					
	TM18	TL96	TL54	TM17	TL74	TL90
Demographic replicate						
Year						0.001
Perceptual range						0.017
Directional persistence	0.347	0.257	0.213	0.439	0.403	0.183
Carrying capacity	50.524	56.358	53.576	50.749	50.232	53.608
Habitat mortality	41.955	37.317	39.436	41.758	41.908	38.699
Demographic replicate: Year	0.002	0.001	0.001	0.002	0.003	0.013
Demographic replicate: Perceptual range						0.001
Demographic replicate: Directional persistence						0.002
Demographic replicate: Carrying capacity						0.001
Demographic replicate: Habitat mortality						0.001
Year: Perceptual range					0.001	0.004
Year: Directional persistence					0.001	0.002
Year: Carrying capacity					0.001	0.005
Year: Habitat mortality					0.001	0.002
Perceptual range: Directional persistence	0.005	0.006	0.008	0.007	0.009	0.006
Perceptual range: Carrying capacity	0.020	0.003	0.001	0.006	0.000	0.002
Perceptual range: Habitat mortality	0.015	0.003	0.004	0.005	0.001	0.003
Directional persistence: Carrying capacity	0.083	0.071	0.043	0.085	0.097	0.026
Directional persistence: Habitat mortality	0.123	0.103	0.114	0.140	0.170	0.056
Carrying capacity: Habitat mortality	6.663	5.736	6.459	6.547	6.890	6.135

Table A1*: The percent (%) of variance in successful dispersers explained by each factor and their two way interactions for baseline landscapes. Only results where variance explained is >= 0.001% are shown.*

Factor	Square					
	TM18	TL96	TL54	TM17	TL74	TL90
Demographic replicate	0.106	0.066	0.180	0.129	0.159	0.112
Perceptual range	0.426	0.248	0.574	0.422	0.480	0.490
Directional persistence	12.582	18.780	15.901	13.822	15.663	16.826
Carrying capacity	15.576	13.193	19.287	16.868	15.720	16.172
Habitat mortality	55.718	47.148	38.663	49.098	56.597	58.020
Demographic replicate: Perceptual range	0.246	0.156	0.236	0.203	0.140	0.240
Demographic replicate: Directional persistence	0.259	0.190	0.188	0.192	0.167	0.125
Demographic replicate: Carrying capacity	0.269	0.128	0.131	0.138	0.058	0.190
Demographic replicate: Habitat mortality	0.085	0.269	0.396	0.273	0.260	0.132
Perceptual range: Directional persistence	0.187	0.098	0.256	0.380	0.580	0.152
Perceptual range: Carrying capacity	0.177	0.222	0.307	0.051	0.419	0.140
Perceptual range: Habitat mortality	0.175	0.093	0.474	0.274	0.226	0.166
Directional persistence: Carrying capacity	0.583	1.916	1.510	0.741	0.221	0.116
Directional persistence: Habitat mortality	1.585	4.786	2.669	3.141	0.534	0.094
Carrying capacity: Habitat mortality	3.933	4.561	6.010	4.352	1.809	0.518

***Table A2**: The percent (%) of variance in the number of isolated patches explained by each factor and their two way interactions for baseline landscapes. Only results where variance explained is >= 0.001% are shown.*

Factor	Square					
	TM18	TL96	TL54	TM17	TL74	TL90
Landscape replicate	0.003	0.004	0.001	0.003	0.004	0.005
Demographic replicate						
Year						
Perceptual range	0.072	0.019	0.007	0.063	0.000	0.015
Directional persistence	0.388	0.311	0.246	0.500	0.444	0.182
Carrying capacity	50.082	55.778	53.079	50.140	49.704	53.096
Habitat mortality	42.267	37.760	39.855	42.210	42.349	39.175
Landscape replicate: Demographic replicate						0.001
Landscape replicate: Year						0.001
Landscape replicate: Perceptual range						
Landscape replicate: Directional persistence						0.001
Landscape replicate: Carrying capacity	0.002	0.002	0.001	0.002	0.002	0.002
Landscape replicate: Habitat mortality	0.001	0.001		0.001	0.001	0.001
Demographic replicate: Year						0.001
Demographic replicate: Perceptual range						
Demographic replicate: Directional persistence						
Demographic replicate: Carrying capacity						
Demographic replicate: Habitat mortality						
Year: Perceptual range						
Year :Directional persistence						
Year: Carrying capacity						
Year: Habitat mortality						
Perceptual range: Directional persistence	0.005	0.007	0.008	0.009	0.010	0.007
Perceptual range: Carrying capacity	0.020	0.006	0.001	0.008	0.000	0.003
Perceptual range: Habitat mortality	0.015	0.004	0.003	0.007	0.001	0.004
Directional persistence: Carrying capacity	0.099	0.087	0.049	0.093	0.101	0.028
Directional persistence: Habitat mortality	0.141	0.117	0.125	0.159	0.173	0.051
Carrying capacity: Habitat mortality	6.701	5.757	6.483	6.576	6.925	6.123

Table A3*: The percent (%) of variance in successful dispersers explained by each factor and their two way interactions for 20% tree removal landscapes. Only results where variance explained is >= 0.001% are shown.*

Factor	Square					
	TM18	TL96	TL54	TM17	TL74	TL90
Landscape replicate	0.007	0.004	0.002	0.002	0.002	0.009
Demographic replicate						
Year						
Perceptual range	0.077	0.030	0.010	0.071	0.000	0.009
Directional persistence	0.433	0.360	0.282	0.576	0.478	0.213
Carrying capacity	49.585	55.140	52.653	49.541	49.240	52.290
Habitat mortality	42.674	38.232	40.209	42.680	42.739	39.849
Landscape replicate: Demographic replicate						0.001
Landscape replicate: Year						0.002
Landscape replicate: Perceptual range						
Landscape replicate: Directional persistence						
Landscape replicate: Carrying capacity	0.003	0.001	0.001	0.002	0.001	0.005
Landscape replicate: Habitat mortality	0.001					0.002
Demographic replicate: Year						0.001
Demographic replicate: Perceptual range						
Demographic replicate: Directional persistence						
Demographic replicate: Carrying capacity						
Demographic replicate: Habitat mortality						
Year: Perceptual range						
Year: Directional persistence						
Year: Carrying capacity						
Year: Habitat mortality						
Perceptual range: Directional persistence	0.005	0.007	0.008	0.009	0.010	0.007
Perceptual range: Carrying capacity	0.022	0.008	0.001	0.010		0.002
Perceptual range: Habitat mortality	0.016	0.005	0.004	0.008	0.001	0.003
Directional persistence: Carrying capacity	0.111	0.102	0.058	0.111	0.107	0.033
Directional persistence: Habitat mortality	0.157	0.132	0.138	0.178	0.180	0.054
Carrying capacity: Habitat mortality	6.694	5.822	6.487	6.572	6.947	6.167

Table A4: The percent (%) of variance in successful dispersers explained by each factor and their two way interactions for 40% tree removal landscapes. Only results where variance explained is >= 0.001% are shown.

	Square					
Factor	TM18	TL96	TL54	TM17	TL74	TL90
Landscape replicate	0.002	0.007	0.002	0.006	0.005	0.075
Demographic replicate						
Year						
Perceptual range	0.082	0.036	0.012	0.075		0.006
Directional persistence	0.492	0.400	0.324	0.621	0.503	0.229
Carrying capacity	49.325	54.559	52.179	49.200	48.886	52.036
Habitat mortality	42.874	38.672	40.608	42.961	43.057	40.004
Landscape replicate: Demographic replicate						0.001
Landscape replicate: Year						0.001
Landscape replicate: Perceptual range						0.001
Landscape replicate: Directional persistence						0.002
Landscape replicate: Carrying capacity	0.002	0.003	0.001	0.004	0.003	0.035
Landscape replicate: Habitat mortality	0.001	0.001	0.000	0.002	0.001	0.021
Demographic replicate: Year						0.001
Demographic replicate: Perceptual range						
Demographic replicate: Directional persistence						
Demographic replicate: Carrying capacity						
Demographic replicate: Habitat mortality						
Year: Perceptual range						
Year: Directional persistence						
Year: Carrying capacity						
Year: Habitat mortality						
Perceptual range: Directional persistence	0.005	0.007	0.008	0.009	0.009	0.006
Perceptual range: Carrying capacity	0.023	0.010	0.001	0.009		0.002
Perceptual range: Habitat mortality	0.017	0.006	0.004	0.009	0.001	0.003
Directional persistence: Carrying capacity	0.128	0.111	0.068	0.114	0.112	0.037
Directional persistence: Habitat mortality	0.181	0.142	0.153	0.191	0.187	0.057
Carrying capacity: Habitat mortality	6.646	5.882	6.490	6.549	6.936	6.057

Table A5: The percent (%) of variance in successful dispersers explained by each factor and their two way interactions for 60% tree removal landscapes. Only results where variance explained is >= 0.001% are shown.

Appendix B

			Square											
			TM18		TL96		TL54		TM17		TL74		TL90	
% of trees removed	Factor	Value	Least squares mean	Standard Error	Least squares mean	Standard Error	Least squares mean	Standard Error	Least squares mean	Standard Error	Least squares mean	Standard Error	Least squares mean	Standard Error
20	**K**	**25**	0.981	0.000837	0.983	0.000930	0.982	0.000618	0.982	0.000951	0.986	0.000963	0.977	0.001389
		50	0.978		0.978		0.978		0.979		0.983		0.974	
		75	0.977		0.975		0.977		0.975		0.977		0.972	
	HM	**0.02**	0.982		0.981		0.982		0.981		0.983		0.977	
		0.035	0.979		0.979		0.979		0.978		0.981		0.974	
		0.05	0.977		0.977		0.976		0.977		0.981		0.971	
	PR	**3**	0.978		0.977		0.978		0.976		0.980		0.973	
		6	0.980		0.980		0.979		0.980		0.983		0.975	
		12	0.979		0.980		0.980		0.980		0.982		0.975	
	DP	**5**	0.977		0.976		0.977		0.976		0.979		0.975	
		7	0.979		0.979		0.979		0.979		0.982		0.974	
		9	0.980		0.982		0.981		0.981		0.985		0.974	
40	**K**	**25**	0.966	0.001414	0.966	0.001004	0.965	0.000790	0.967	0.000857	0.975	0.000795	0.955	0.001550
		50	0.959		0.958		0.958		0.959		0.968		0.943	
		75	0.953		0.951		0.955		0.950		0.959		0.935	
	HM	**0.02**	0.963		0.963		0.964		0.962		0.970		0.949	
		0.035	0.959		0.958		0.959		0.958		0.966		0.944	
		0.05	0.956		0.955		0.955		0.955		0.965		0.940	
	PR	**3**	0.958		0.954		0.957		0.955		0.965		0.941	
		6	0.960		0.961		0.960		0.960		0.969		0.947	
		12	0.959		0.960		0.961		0.960		0.968		0.945	
	DP	**5**	0.955		0.953		0.955		0.952		0.963		0.943	
		7	0.960		0.959		0.959		0.959		0.968		0.944	
		9	0.962		0.963		0.963		0.964		0.971		0.946	
60	**K**	**25**	0.951	0.000700	0.950	0.001388	0.946	0.000916	0.953	0.001092	0.964	0.001208	0.930	0.003804
		50	0.940		0.941		0.937		0.940		0.954		0.915	
		75	0.933		0.931		0.931		0.926		0.940		0.904	
	HM	**0.02**	0.945		0.948		0.946		0.943		0.956		0.920	
		0.035	0.941		0.940		0.937		0.939		0.952		0.917	
		0.05	0.938		0.935		0.931		0.937		0.950		0.912	
	PR	**3**	0.940		0.935		0.935		0.936		0.949		0.911	
		6	0.943		0.944		0.939		0.942		0.954		0.919	
		12	0.942		0.943		0.940		0.942		0.954		0.918	
	DP	**5**	0.936		0.934		0.932		0.932		0.947		0.914	
		7	0.942		0.941		0.939		0.941		0.953		0.917	
		9	0.947		0.947		0.944		0.946		0.957		0.918	

Table B1: Proportion of successful dispersers least squares means for the four varied factors (Carrying capacity, Habitat mortality, Perceptual range, Directional persistence) extracted from linear mixed models with landscape replicate included as a random effect. PR=perceptual range, DP=directional persistence, K=carrying capacity, HM = matrix per step mortality risk.

			Square											
			TM18		TL96		TL54		TM17		TL74		TL90	
% of trees removed	**Factor**	**Value**	**Least squares mean**	**Standard Error**	**Least squares mean**	**Standard Error**	**Least squares mean**	**Standard Error**	**Least squares mean**	**Standard Error**	**Least squares mean**	**Standard Error**	**Least squares mean**	**Standard Error**
20	**K**	**25**	0.269	0.036212	0.245	0.037796	-0.051	0.021747	0.324	0.033635	-0.019	0.031792	0.146	0.033427
			0.100		0.164		-0.076		0.198		0.014		0.147	
		50	0.077		0.259		0.020		0.163		0.075		0.186	
		75	0.040		0.019		-0.026		0.065		0.020		0.004	
	HM	**0.02**	0.225		0.311		-0.050		0.297		0.091		0.138	
		0.035	0.180		0.339		-0.032		0.323		-0.042		0.338	
		0.05	0.161		0.296		-0.054		0.216		0.032		0.123	
	PR	**3**	0.135		0.100		0.021		0.290		0.027		0.303	
		6	0.149		0.273		-0.076		0.179		0.010		0.054	
		12	0.236		0.326		-0.097		0.400		0.038		0.202	
	DP	**5**	0.059		0.247		0.071		0.229		0.029		0.123	
		7	0.151		0.095		-0.081		0.056		0.002		0.154	
		9	0.531	0.037096	0.524	0.048904	-0.040	0.024873	0.388	0.035681	-0.041	0.03253	0.336	0.032991
40	**K**	**25**	0.347		0.352		-0.075		0.366		0.087		0.389	
		50	0.270		0.472		0.006		0.345		0.177		0.487	
		75	0.125		0.099		-0.049		0.096		0.057		0.061	
	HM	**0.02**	0.452		0.494		-0.068		0.463		0.140		0.441	
		0.035	0.572		0.755		0.007		0.540		0.026		0.710	
		0.05	0.405		0.509		-0.053		0.346		0.076		0.345	
	PR	**3**	0.380		0.375		0.015		0.418		0.067		0.537	
		6	0.364		0.465		-0.072		0.335		0.081		0.330	
		12	0.619		0.834		-0.116		0.655		0.090		0.559	
	DP	**5**	0.259		0.321		0.077		0.309		0.090		0.342	
		7	0.270		0.193		-0.070		0.135		0.044		0.311	
		9	0.594	0.044337	0.632	0.049542	0.046	0.039228	0.639	0.046316	-0.046	0.035682	0.544	0.043359
60	**K**	**25**	0.497		0.433		-0.046		0.566		0.041		0.551	
		50	0.412		0.529		0.035		0.584		0.108		0.736	
		75	0.204		0.087		-0.089		0.234		-0.045		0.113	
	HM	**0.02**	0.616		0.580		-0.065		0.765		0.116		0.653	
		0.035	0.684		0.927		0.189		0.790		0.031		1.066	
		0.05	0.509		0.651		0.001		0.609		0.044		0.587	
	PR	**3**	0.534		0.396		0.068		0.634		0.021		0.700	
		6	0.461		0.547		-0.034		0.546		0.037		0.544	
		12	0.748		0.951		-0.022		0.946		0.147		0.850	
	DP	**5**	0.376		0.451		0.094		0.552		-0.019		0.533	
		7	0.380		0.192		-0.038		0.290		-0.025		0.449	
		9												

***Table B2**: Increase in the number of isolated patches least squares means for the four varied factors (Carrying capacity, Habitat mortality, Perceptual range, Directional persistence) extracted from linear mixed models with landscape replicate included as a random effect. PR=perceptual range, DP=directional persistence, K=carrying capacity, HM = matrix per step mortality risk.*